

THE MOLTING CYCLE OF THE SPINY LOBSTER, *PANULIRUS ARGUS* LATREILLE. I. MOLTING AND GROWTH IN LABORATORY-MAINTAINED INDIVIDUALS¹

DOROTHY F. TRAVIS²

*Bermuda Biological Station for Research*³

Since the summer of 1949, the author has become deeply interested in the physiology of molting and growth in the Bermuda spiny lobster, *Panulirus argus* Latreille. Investigations have been concerned with normal morphological and physiological changes related to molting and growth in this animal. Interest has centered around the changes which occur in the skeleton, tissues, blood, and urine of normal animals during the molting cycle.

The present paper, the first of a series, is concerned with the spectacular process of molting, the mechanics by which it is achieved, some physical factors influencing molting and growth, and growth determined by weight and length in laboratory-maintained spiny lobsters.

MATERIALS AND METHODS

Male and female spiny lobsters, ranging in carapace length from 20–92 mm., were generously supplied by the Bermuda Biological Station and Dr. W. H. Sutcliffe, who furnished the author with all immature forms from his catches of 1952. Only twenty-seven of approximately 500 animals supplied were of the carapace length range of 90–92 mm. These animals were included in the data for Figure 11. No further use was made of these animals following the first laboratory molt because Sutcliffe (1952, 1953) has pointed out that sexual maturity in females is attained some time after the carapace length reaches 90 mm. Information was almost exclusively limited, therefore, to animals of 20–89 mm. carapace length. All animals, when brought into the laboratory, were numbered with a lead or plastic tag, wired to the base of an antenna. Their number, sex, weight and carapace length were recorded. The animals were then placed in concrete tanks of running sea water (22' × 3' × 1½'). By partitioning portions of the sea water tanks with plastic screens, premolt animals could be isolated from the others. At the time of ecdysis animals were placed in individual aquaria or in partitioned portions of the tanks. Following ecdysis, animals were allowed to harden before being placed in partitioned

¹ This work was supported in part by an Atomic Energy Commission Postdoctoral Fellowship from the University Relations Division, Oak Ridge Institute of Nuclear Studies. The author wishes to express her sincere appreciation to Dr. John H. Welsh, Dr. Emery F. Swan, Dr. W. H. Sutcliffe, and Dr. E. E. Mortensen for the many helpful criticisms and suggestions they have made regarding this manuscript.

² Present address: Department of Zoology, University of New Hampshire, Durham, New Hampshire.

³ Contribution No. 214.

portions of tanks in different size groups. The laboratory history of each animal was followed closely throughout the period of observation by the method described. The method of designating stages in the molting cycle by letters A, B, C, D (Drach, 1939), as well as the method by which the molting cycle is divided into stages by daily intervals, was used.

The weights of animals throughout the molting cycle were obtained by carefully placing them on paper towels and drying them as thoroughly as possible. The animals were then rolled in a piece of nylon screen which restricted their movements while being weighed on a triple beam balance, accurate to 0.3 gm.

Length measurements were made with a vernier caliper from the mid-dorsal anterior point between the two rostral spines to the most posterior mid-dorsal point of the carapace.

In all cases where the standard error of the arithmetical mean was calculated, the method of Fisher (1948) for small samples was used.

With few exceptions, all animals were fed every other day. Their laboratory diet consisted of fish fry, anchovies, small pieces of larger fish, molluscs, and ground beef when the bait supply became low during the winter months.

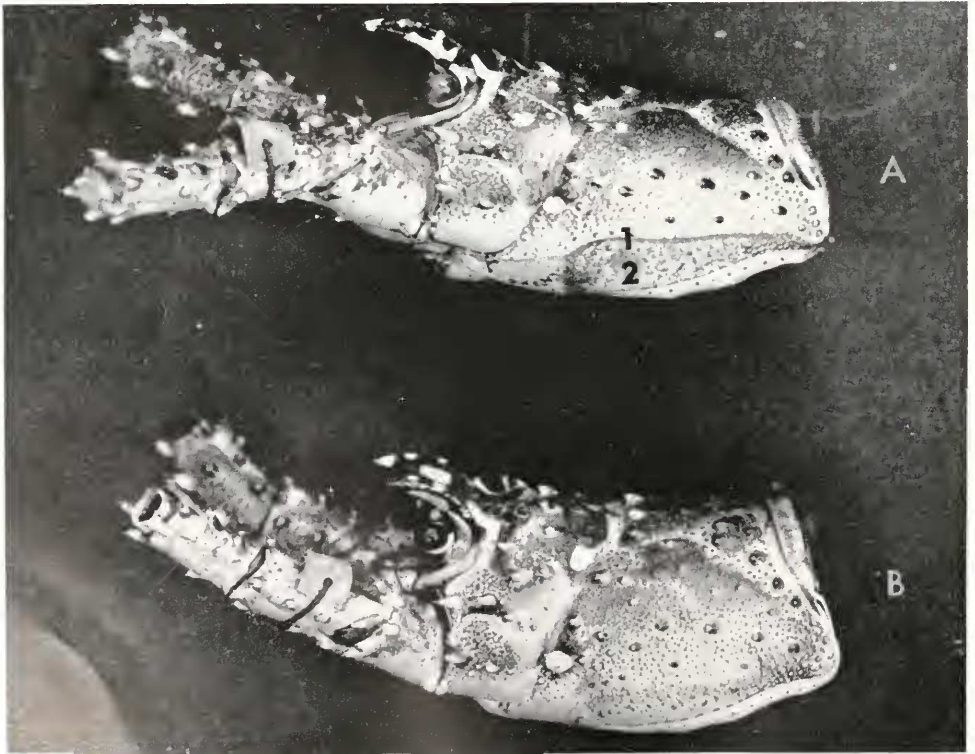


FIGURE 1. The shed (A) and hard carapace (B) of *Panulirus argus*. In the exuvium, the resorption or ecdysial line (1) and the area ventral to this, in which somewhat less resorption occurs (2), will be noted. Neither the ecdysial line nor the softened area ventral to the line will be noted in the hard carapace, which was removed from an animal in Stage C of the molting cycle.

OBSERVATIONS AND DISCUSSION

In *Panulirus argus*, a premolt animal can easily be detected by the appearance of a resorptive or ecdysial line along the branchiostegites (Fig. 1). This line becomes clearly evident 3-4 days preceding ecdysis in the summer months. Beneath this resorptive line appreciable softening (20% resorption—Travis, 1951a) of the whole ventral area occurs. Premolt animals can thus be detected by feeling this softened area even before the resorptive or ecdysial line is clearly evident. In the winter months, premolt animals can be detected by touch as early as 14-21 days

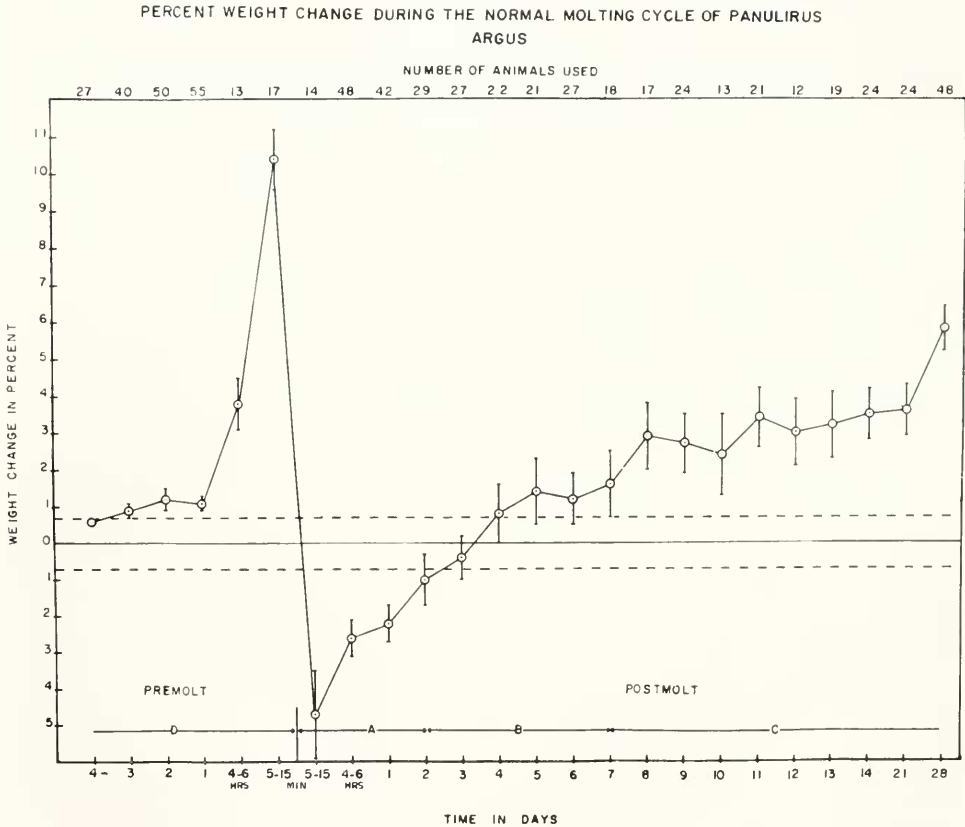


FIGURE 2A. The per cent weight change during the normal molting cycle of *Panulirus argus*. The number of animals used per point on the graph is indicated along the top ordinate. All points represent the mean arithmetical values obtained from the number of animals specified. The vertical lines represent plus or minus the standard error of the mean. The solid horizontal line marked by (o) on the graph, represents the base weight (intermolt weight) upon which per cent changes were calculated. Dashes above and below the solid horizontal line represent the standard daily variation in weight of 24 animals. This daily variation was observed over a 7-day interval during the intermolt period, a time at which the weight of the animals is stable. The vertical line at the bottom of the graph separates the premolt and postmolt period. The bottom ordinate represents the time in days preceding and following molting. The solid horizontal lines parallel to the bottom ordinate and broken by the letters D, A, B, and C designate the four major stages in the molting cycle as utilized by Drach, 1939.

preceding ecdysis. The lengthening of the premolt period is brought about by lower winter temperatures, which markedly slow down physiological activities associated with the molting process.

One of the most manifest external changes noted a few hours before ecdysis in *Panulirus* is the swollen condition of the intersegmental membranes separating the cephalothorax and abdomen. Due to resorption from the resorptive or ecdysial line, along the branchiostegites, and resorption from an articulating condyle connecting the branchial chamber to the posterior edge of the branchiostegites, lateral expansion of the soft body beneath the old skeleton is allowed. Such swelling and lateral expansion of the thorax immediately preceding ecdysis were first thought

TABLE I

The per cent water absorbed and per cent weight increases preceding molting. Values are based on normal changes in weights associated with ecdysis in Panulirus argus. The abbreviations of Guyselman (1953) are used in this table

Number of animals used	Weight in grams						E as $\frac{E}{W_1}$ of W_1	W_3 as $\frac{W_3}{E}$ of I	W_1 as $\frac{W_1}{E}$ of I
	I	W_1	E	E_1	W_2	W_3			
3	519.2-539.4	571.7-596.4	92.7-124.0	50.5-55.8	511.2-544.0	40.3-70.0	15.6-21.7	7.5-13.5	10.1-11.6
Avg.	528.5	584.4	111.9	53.0	524.1	51.9	19.2	9.8	10.9
3	623.3-668.9	663.5-730.1	103.3-140.5	56.0-65.2	620.0-663.5	30.8-73.9	15.6-19.2	4.7-11.0	6.5-9.3
Avg.	647.9	704.2	124.5	60.6	636.5	56.9	17.6	8.8	8.3

I = Wet weights of intermolt animals

W_1 = Wet weights of animals 15 minutes preceding molt

E = Wet weights of exuviae

E_1 = Dry weights of exuviae

W_2 = Wet weights of animals 15 minutes following molt

$W_3 = W_2 - (W_1 - E)$ = Weight of water absorbed in a period taken between 15 minutes preceding to 15 minutes following molt

E as $\frac{E}{W_1}$ of W_1 = The weight of the exuviae, expressed as per cent of the total premolt wet weight of the animals

W_3 as $\frac{W_3}{E}$ of I = The weight of the water absorbed expressed as percentage of the previous intermolt wet weight

W_1 as $\frac{W_1}{E}$ of I = Total premolt weight increase expressed as per cent of the previous intermolt wet weight

to be entirely due to the absorption of water. This has not proved to be the case and will be discussed in a subsequent section of this paper. In a search for the causal mechanisms immediately involved in molting, a number of factors were considered. These were weight changes, water uptake, and possible structures involved in water retention.

Weight changes

In *Panulirus*, marked changes in body weight are observed immediately preceding ecdysis and for a four-week period following it. These wet weight changes, expressed as per cent of the previous intermolt weights, were followed throughout the normal molting cycle of the spiny lobster and are shown in Figure 2A. It will be observed in the 80-89 mm. carapace length animals, represented in this graph, that little change in weight is noted in the pre-ecdysial period until the day preceding ecdysis. At this time, the first significant weight increase is observed a

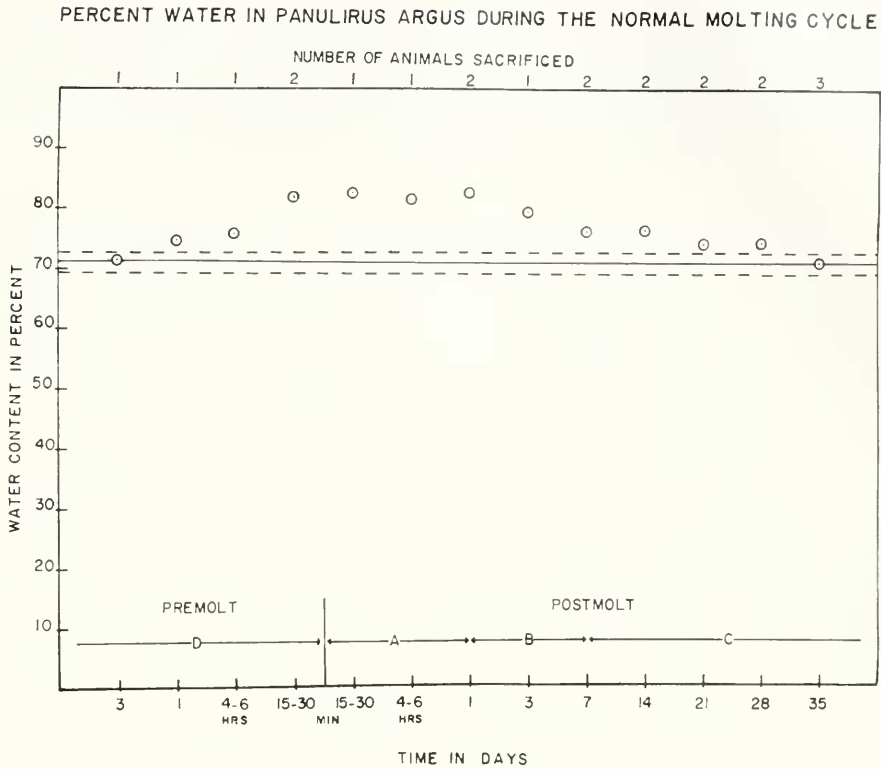


FIGURE 2B. Changes in water content of *Panulirus argus* during the normal molting cycle. Dashes above and below the horizontal line indicate plus or minus variations from the intermolt mean.

few hours preceding molting. The weight of the animals continues to increase to a peak premolt value of around 10%. This peak premolt value is attained 5 to 15 minutes preceding ecdysis. The marked increase in weight attained at this time is primarily the result of water absorbed.

During the early post-ecdysial period (15 minutes) a striking weight loss is observed. This weight loss of almost 16% is primarily due to the loss of the old exuviae, which constitute from 15.6 to 21.7% of the total premolt wet weight of the animal (Table I). Within 4 to 6 hours, however, the weight begins to rise. This continues at a rather steady pace, reaches the intermolt value two to four days following molt, significantly rises above this level at eight days, tends to level off and reaches the new intermolt value between 28 and 35 days.

Water uptake

It was mentioned earlier that the peak premolt weight increase of 10% was the result primarily of water absorbed. This is indicated in Table I. Here the weight of the water absorbed preceding molt is determined (Drach, 1939; Guyseman, 1953) and expressed as per cent of the previous intermolt wet weight. The premolt weight increase, expressed as per cent of the previous intermolt wet weight

determined as indicated in the previous section, is also listed. The weight of water absorbed and the total premolt weight increase, both obtained by two different procedures (Table I), compare favorably. Weight increases preceding molting, therefore, are entirely due to water absorbed. This is evident both in animals within the 500 gram range and those in the 600 gram range.

Water content

The water content of the animals, expressed as per cent, was determined from the wet and dry weights of individuals sacrificed at various intervals throughout the molting cycle. It will be observed (Fig. 2B) that the water content of an intermolt animal (late stage C) is 71.0%. The water content of *Panulirus* begins to increase the day preceding molt (74.7%), rises to 81.3% fifteen minutes preceding molt, and reaches a peak value of 82.4% one day following molt, 11.4% above the intermolt value of 71.0%. It should be pointed out here that the increase in water content of individuals sacrificed 15–30 minutes preceding molt (Fig. 2B) is in agreement with the weight increase observed in Figure 2A and the calculated per cent water absorbed in this same period (Table I). Since presumably all mineral and organic resorption is completed in the old skeleton at 15–30 minutes preceding ecdysis, the wet and dry weights of these skeletons must be subtracted from the total wet and dry weights of the animals with their old skeletons, to obtain the true water content of the animals alone. If this is not done the weight increase of 10% is observed (Fig. 2A) with no rise of corresponding magnitude in water content, which is represented in Figure 2B. Because all animals used in Figure 2B were sacrificed for dry weight determinations, the average per cent of the total weights of the animals due to exuviae, both wet and dry weights, was calculated from values given in Table I. These values were then applied to the two animals sacrificed 15–30 minutes preceding molt (Fig. 2B) to obtain the presumed wet and dry weights of the old skeleton of these animals. The water content of these animals, without their old skeletons, was then calculated. From three days following molt the water content slowly declines, but does not return to its intermolt range of 71.0% before 21 to 28 days. It might be mentioned that at 28 days the animals have fully calcified their new skeletons (the principal layer and the membranous layer are fully formed), weight stability is reached, and apparently all growth of soft tissues is completed. It would appear from Figure 2B that water absorption is not completed for at least two weeks following molting. This is perhaps a false impression one might obtain at first observation. Although the water content is above the late Stage C value, it must be remembered that growing tissue is gradually replacing water absorbed at and following molt. Water absorption in *Panulirus* is probably completed the day following molt. This is in agreement with the situation observed in *Maia squinado*, *Carcinides macnas*, and *Cancer pagurus* (Drach, 1939) in which water absorption apparently is completed within 6 to 12 hours or less following molt.

MECHANISMS INVOLVED IN SWELLING AND LATERAL EXPANSION OF THE THORAX IMMEDIATELY PRECEDING ECDYSIS

Since the animals increase their body weight approximately 10% before molting and since this increase is entirely accounted for by uptake of water, the question

arises as to how this water enters the organism. Two possible structures which might be involved in water retention were studied with the idea of obtaining evidence of the cause of the greatly expanded and swollen thorax, which results ultimately in the lifting of the exuviae at ecdysis. The major structures considered were the membranous layer of the old skeleton and the stomach.

The membranous layer

The homogenous non-laminated layer which is attached to the inside of the exuviae, observed by Vitzou (1882), Herrick (1895), Yonge (1932), and called the membranous layer by Drach (1939), was investigated as a possible site of water retention. It might be added that this layer holds large amounts of water after the exoskeleton is shed and appears to swell because of water absorption from the medium. Weight changes were followed in two premolt animals. From one animal (A) the membranous layer was removed at one day preceding molt, at which time no marked change in body weight had occurred, while in the other (B) the membranous layer was removed when the animal had increased its body weight 8% preceding molt. Wet and dry weights of pieces of this layer (as close to 2 cm², in size as possible) were obtained and per cent water in each piece compared. A difference in water content of the two pieces might indicate whether this structure is involved in water retention. It was found, however, that the water content in (A) was not appreciably different from that of (B). Therefore the idea that water retention by the membranous layer may contribute to weight changes preceding molt was abandoned.

The stomach

The stomach was then considered as a site for water uptake and retention preceding molt. Drach (1939) demonstrated in crabs that absorption of water during the course of shedding and shortly following occurs primarily through the gut. The stomach becomes turgid and greatly swollen during this period and in *Panulirus* swells to the extent that it occupies over half of the cephalothorax. This would cause pressure to be exerted on the surrounding regions and is, in all probability, the actual cause of swelling and lateral expansion of the thorax. Drach (1939) attributed the turgidity and swelling of the stomach in *Maia squinado* and *Cancer pagurus* to the water held in the stomach and digestive tube during shedding. He was able to remove a considerable quantity of water from the stomach of these animals, shortly preceding ecdysis, and within a short interval removal of a large quantity was again possible. In an attempt to withdraw water from the stomach of *Panulirus*, 10 premolting animals were selected. As the animals increased their weights preceding ecdysis, attempted withdrawal of water from the stomach, by inserting a cannula into the stomach via the esophagus, proved fruitless. Even when the increase in body weight had reached 8% a few minutes preceding ecdysis, little water could be withdrawn. No more than 0.5 cc. could ever be withdrawn. In three cases, animals were weighed until the body weight increased by 8–10% and then sacrificed. The old and new skeleton overlying the stomach were removed. A syringe needle was inserted in the turgid stomach in an attempt to withdraw fluid. No fluid was present. On the contrary, it was

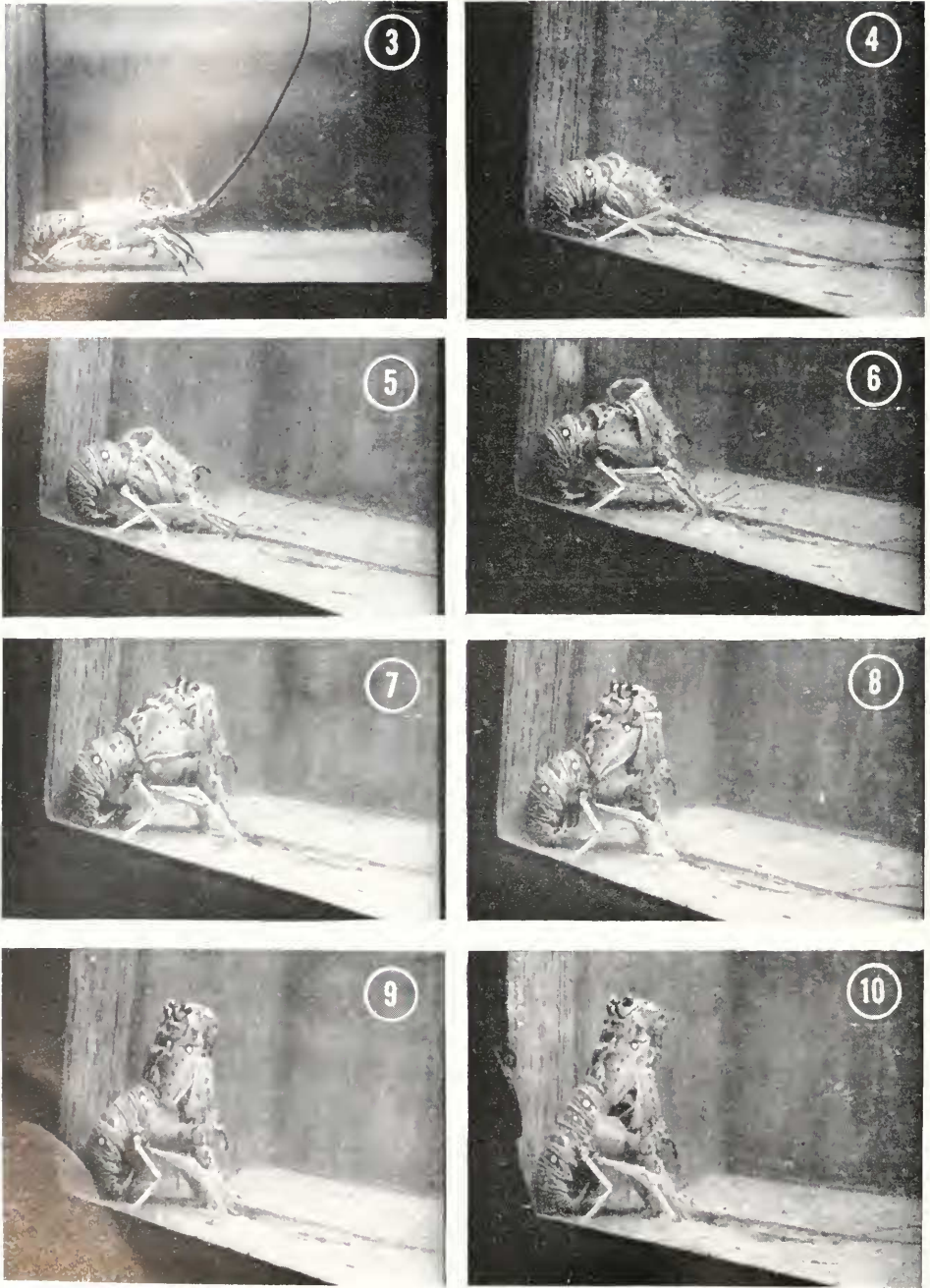


FIGURE 3. Ecdysis in *Panulirus*. The animal seeks out a suitable place to shed.
FIGURE 4. The tail is flexed; the thorax is lowered on the substratum with antennae and antennules braced and extended to facilitate forward bracing of the animal, while the last pair

found that the turgidity and swollen condition was due to the presence of gas of unknown composition which appeared to be between the old stomach lining and the new. Following the puncture of the new outer layer with a syringe needle the wound closed and the stomach again swelled. An incision in this layer caused the stomach to collapse. The "balloon" condition of the new stomach causes the new soft body to expand in the thoracic region and is without doubt the immediate mechanism which lifts the old carapace at ecdysis. Such a mechanism would also account for the increase in volume of the emerging animal.

Water absorbed preceding ecdysis is probably taken in primarily through the gills and the soft intersegmental membranes. It does not appear to be taken in through the digestive tract. Hydration of the tissues probably occurs during the late pre-ecdysial as well as post-ecdysial period. This hydration of the tissues has been indicated by Baumberger and Olmstead (1928) in *Pachygrapsus crassipes* and is suggested by the recent work of Kincaid and Scheer (1952) on *Hemigrapsus nudus*. It is pertinent to add that the former workers showed that there was a rise in the internal osmotic pressure preceding molt. This peak in osmotic pressure is presumably caused by an increase in osmotically active constituents (organic acids) which accumulate in the hemolymph as a result of the breakdown of fats and glycogen, abundant in the hepatopancreas during the premolting period of all Crustacea investigated. The increase in osmotic pressure preceding molt would therefore account for increased water absorption preceding and immediately following molt. Increased water uptake causes the osmotic pressure to fall sharply following molt and to return gradually to normal as the skeleton of the animal hardens. A study of the green glands during the pre-ecdysial period should be made. It is quite possible that antidiuresis might occur during the few hours preceding ecdysis. Such water retention could also serve as one of the correlatives contributing to the marked increase in weight of the animal during this time. Furthermore, it is

of walking legs is extended behind and serves as the hind bracing elements. The old carapace has begun to lift, making visible the new skeleton below the old branchiostegites.

FIGURE 5. A further stage during ecdysis showing the progressive lifting of the old carapace.

FIGURE 6. At this stage the animal has raised the thorax off of the substratum and the old carapace has lifted about 45° from its original position.

FIGURE 7. At this stage of ecdysis the animal has raised itself considerably from the substratum with the tail gently flexed. The old carapace has lifted and has tilted at an angle of 90° from its original position. The thorax of the animal is almost completely freed, making visible the new eyes and rostral spines. During this stage of ecdysis, the old branchial chamber becomes evident ventral to the new branchiostegites. It is interesting to note that the abdomen begins to undergo contractions in a telescopic fashion, i.e., segments begin to telescope and extend. Freeing of the abdomen occurs in this manner.

FIGURE 8. A further stage in ecdysis. The animal has raised itself considerably from the substratum by arching its soft cephalothorax. The old branchial chamber is almost completely freed. The new antennae are just beginning to appear and two new abdominal segments are free.

FIGURE 9. In this stage of ecdysis, the animal has arched its soft cephalothorax almost 90° from its original position, three new abdominal segments are freed, the fourth beginning to appear and the new antennae are much more evident. The new 5th walking leg may be observed between the old gill chamber, old branchiostegites and the new.

FIGURE 10. The last stage of ecdysis, a second or so before the animal gives one sudden flexion and extension of the abdomen freeing itself completely from the old skeleton. It will be noted that four new segments are visible, the new proximal portions of the antennae and the new fifth walking leg are clearly evident.

possible that changes in salt excretion by the green glands might also be a factor in raising the osmotic pressure prior to molting.

Ecdysis

All of the changes observed in the premolt period lead to shedding of the exoskeleton. This is depicted in Figures 3-10. For a period of at least two hours preceding ecdysis, the spiny lobster undergoes exercise movements. These include flexing of the abdomen under the thorax and bumping it along the substratum; lowering of the thorax on the substratum while raising and extending the abdomen rigidly; lunging movements with sudden stops. These are all movements to facilitate loosening of the old skeleton from the new. Following such movements, the animal seeks a suitable place to shed (Fig. 3). The tail is then flexed; the thorax is lowered on the substratum with antennae and antennules lowered and extended to facilitate forward bracing of the animal, while the last pair of walking legs is extended behind and serves as the hind bracing elements (Fig. 4). In this position, little movement is observed other than slow contractions of the soft body beneath the old carapace. As these slow contractions occur the old carapace begins to lift at the intersegmental membrane between carapace and abdomen, making visible the new skeleton below the old branchiostegites (Figs. 4, 5). It should be pointed out again that the resorptive or ecdysial line serves as a hinge. The resorption from, and loosening of, an articulating condyle, which attaches the branchial chamber to the inner posterior edge of the branchiostegites, allow the soft body to expand in width (Figs. 5, 10). There is no breaking along the resorptive line of *Panulirus argus* as Crawford and De Smidt (1922) and Smith and Gatham (1948) thought. As the eyes are withdrawn from their old skeleton, the carapace lifts considerably (Fig. 7). At this time (Figs. 7, 10) the segments of the abdomen begin to move in and out in a telescopic fashion, thus freeing themselves from the old skeleton. As the animal pulls itself free from the old carapace it raises itself from the substratum by arching its soft cephalothorax (Figs. 8, 10). The rostral spines and eyes appear, while the old gill chamber can be seen ventral to the new branchiostegites (Figs. 7, 10). The antennae are then pulled free of the old skeleton (Figs. 8, 10). Newly withdrawn legs may be observed between the gill chamber and branchiostegites of the old skeleton (Figs. 9, 10). Three abdominal segments are observed free of the old (Fig. 9). A later stage (Fig. 10) indicates how the animal frees itself from the old skeleton. Here four abdominal segments are freed and the legs are more clearly observed above the old gill chamber between the new and old branchiostegites. The animal raises itself much above the old skeleton while pulling itself free. At this stage the animal suddenly flexes and then extends the abdomen, freeing it completely from the old skeleton. The actual time required for the entire process of ecdysis averages from 3-5 minutes for the 70-79 mm. animals depicted. The larger animals, 80-89 mm., require from 5-10 minutes. Immediately following ecdysis the animal moves about vigorously. Expansion of the flattened appendages is accomplished in this manner. By such movements, blood rushes into the appendages and causes them to assume their normal shape.

Following molting, these animals were allowed to remain isolated from all others through Stage A and B (a period of 5-6 days) at which time they begin to feed, their skeleton attains a parchment-like consistency, and they are capable of

protecting themselves. By 7–12 days (Stage C) the branchiostegites have hardened and complete hardening of the skeleton by deposition of minerals therein occurs within approximately four weeks.

FACTORS INFLUENCING MOLTING

Temperature

In Bermuda where average monthly water temperatures range from approximately 17° in February to 29° C. in August, the range would appear to be sufficiently great to stimulate *Panulirus argus* to molt seasonally. Very little molting occurs in the months of December–April, during which time the water temperatures are lowest (Fig. 11 and Table II). It might be added that the temperature of tank water is within a few tenths of a degree of that recorded at the nearby tide station. A water temperature of 22° C. or slightly over in the spring is sufficient to initiate molting (Fig. 11). As water temperatures approach 23° C. the number of molting individuals rises from below 10% to well above. This rise begins in May and increases throughout the summer months with the peak of molts occurring in June, July, August and September, at which time the highest water temperatures of 28°–30° C. are reached. The number of molting individuals, during

THE INFLUENCE OF WATER TEMPERATURE ON MOLTING IN *PANULIRUS ARGUS* LATREILLE

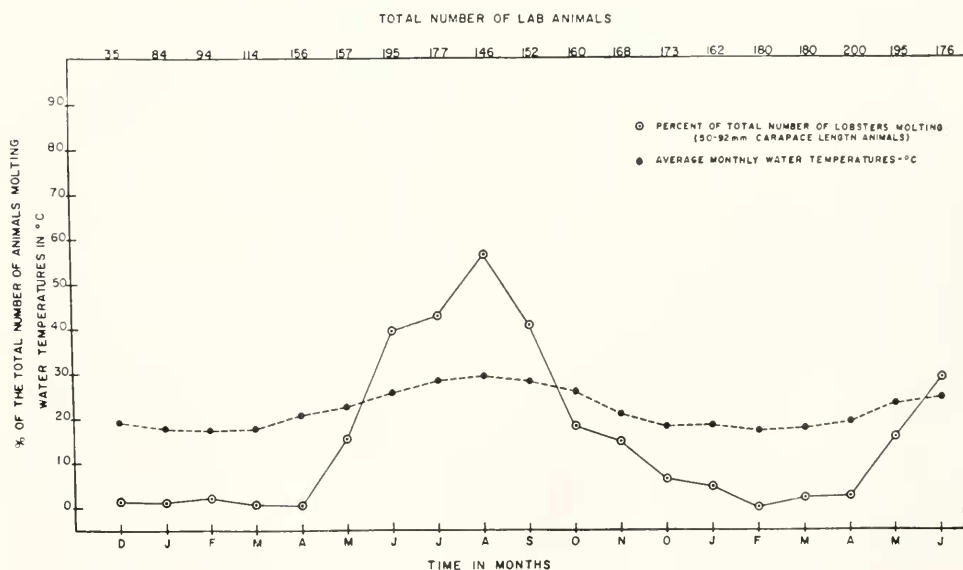


FIGURE 11. The influence of water temperature on molting in *Panulirus argus*. The total number of animals in the laboratory population in any given month is indicated along the top ordinate while the respective months are indicated along the bottom ordinate. Along the Y-ordinate water temperature in ° C. and per cent of the total number of animals molting are indicated. The per cent of molting individuals is plotted with mean temperatures against time in months.

late fall, begins to decline as temperatures decrease, and in the month of December (temperature range $48-20^{\circ}$) less than 10% of the total laboratory population molts. Water temperatures of 17° – 18° C. virtually stop the process. The influence of the water temperatures on molting has been pointed out by Templeman (1936a, 1936b, 1940), Drach (1939, 1949), and Truitt (1939). The quantity of food required by the animals also depends largely upon the temperature. When the water temperature is low the food requirement of the animals is low. Their metabolism is greatly accelerated with a rise in water temperature. Other factors, such as photoperiodism, lunar phases, tides, and salinity of the water which might possibly influence molting, have not been investigated by the author. Templeman (1936b), however, in addition to showing that at high water temperatures larval American lobsters molted more frequently than in colder waters, found that salinities as low as 21 parts per mille were only slightly less favorable than the normal

TABLE II

Intermolt periods of 80–89 mm. carapace length animals during a period of one year

Month of molt	Number of animals molting	Intermolt periods in days	Average monthly Temperature, $^{\circ}$ C.
January	3	161 ± 1	17.9
February	0	No molts	17.4
March	0	No molts	17.8
April	1	73	20.7
May	10	67 ± 2	22.8
June	17	68 ± 2	25.9
July	13	60 ± 4	28.4
August	11	142 ± 8	29.2
September	10	201 ± 6	28.1
October	5	232 ± 5	26.0
November	5	213 ± 2	21.0
December	0	No molts	18.2

31 parts per mille. Larvae reared in total darkness molted earlier than those reared in light, were larger, and had a higher survival rate than those reared in light. He also found (1940) that egg-laying in American lobsters was retarded by cold.

It will be noted from Table II that the intermolt or growth periods are the shortest in animals molting in the months of May, June, and July. These animals, after molting in the respective months, are subjected to gradually rising temperatures and molt again within 60–70 days. Although the highest average monthly temperature occurs in August, animals molting in this month will be subjected to gradually falling temperatures in the following months. As a consequence, their metabolism is slowed down, feeding becomes less, and their intermolt periods are prolonged. This is likewise true of animals molting in September, October, November, and January. The growing period of the Bermuda lobster therefore appears to be limited effectively to a period of approximately seven months in the laboratory (the months during which the water temperatures are highest). Very little molting and growth occur in the population during the months of December

through April (the months during which the water temperatures are lowest). Sutcliffe (personal communication) has indicated that the two foregoing statements are also, in general, applicable to the field population.

Although the summer intermolt periods (Table III) are shorter in smaller than in larger animals, the actual number of molts observed during a period of one year in four of the size groups maintained in the laboratory proved to be approximately the same. Generally four molts per year were observed in these groups. This again appears to be due to the fact that the intermolt periods are prolonged following the August molt. As winter months approach, the smaller as well as the larger sexually immature animals cease to molt and grow.

The influence of size on molting

From the foregoing, water temperature does appear to be largely responsible in *Panulirus argus*, for: (1) The onset of molting; and (2) the frequency of molting and therefore the rate of growth. It is apparent that the rate of growth varies from one size group to the next. The smaller the individuals, the more frequently they molt or the more rapid are their growth rates. This was determined by

TABLE III

Average summer intermolt periods of various size lobsters molting in May, June and July

Number of animals	Carapace length	Average summer intermolt period \pm Standard Error of the Mean	Theoretical number of molts per year in the laboratory based on yearly intermolt periods and growing time	Actual number of molts observed in animals maintained for one year
41	80-89	65 \pm 1	3-4	3-4
42	70-79	56 \pm 1	3-4	3-5
25	60-69	55 \pm 2	3-4	3-4
5	50-59	51 \pm 2	4-5	4
4	40-49	41 \pm 1	5	Not carried for one year
11	30-39	44 \pm 3	5	Not carried for one year
29	20-29	40 \pm 2	5	Not carried for one year

noting the summer intermolt periods of each size group maintained in the laboratory (Table III). It is evident from Table III that as animals increase in size their intermolt periods are longer or the frequency of shedding decreases. In small animals, the rate of growth is rapid and it decreases progressively as they approach sexual maturity. Kinoshita (1934), Nakamura (1940), Templeman (1940), Challenger (1943), Pearson and Anderson (1946), and Bradstock (1950) have also noted that young lobsters of several species (*Panulirus japonicus*, *Homarus americanus*, *Panulirus interruptis*, and *Jasus lalandi*) molt more frequently than old ones.

GROWTH IN LABORATORY-MAINTAINED ANIMALS

Before discussing growth of laboratory-maintained spiny lobsters, it should be pointed out that this information cannot represent exactly the growth of animals

under natural conditions, for laboratory conditions, at best, do not truly duplicate the field situation.

The following information was obtained to serve as a basis for future studies concerning hormonal factors which influence molting and growth in the Bermuda spiny lobster.

Growth by weight

Weight stability is reached several weeks following a molt. The length of this period depends upon size of the animals and the season of the year. No attempt was made in these sexually immature animals to separate the data on the basis of sex. Growth in weight is one of the most important means of studying many aspects of the molting cycle, such as determining the per cent water in the animals, the amount of water absorbed, and per cent weight change throughout the molting cycle (discussed in a previous section of this paper.) Special care, however, must be taken in handling Crustacea while following individuals through their cycle, because the antennae and periopods may be autotomized. If such happens, these animals can no longer be used for subsequent weight changes. Autotomy can generally be avoided by draining the large concrete tanks and by carefully lifting each individual out of the drained tanks for weighings.

TABLE IV
Per cent growth by weight per molt during the summer months

Number of animals	Carapace length (mm.)	Mean per cent growth by weight per molt \pm standard error of the mean	Calculated per cent growth per year based on number of molts per year (Tables III, VI)	Weight stability is reached in the summer days post molt
48	80-89	5.8 ± 0.6	17-23	28-35
33	70-79	8.4 ± 1.0	25-34	28
22	60-69	10.0 ± 1.1	30-40	28
20	50-59	14.9 ± 1.7	60-75	21-28

The weight changes of the 80-89 mm. carapace length animals were observed throughout the molting cycle (Fig. 2A). These weight changes are expressed as per cents of the previous intermolt weights. The per cent growth by weight of these larger animals, throughout the summer months, indicates that they increase their body weight on the average approximately 6% per molt in the laboratory. From Table IV it will be observed that the smaller the animals, the greater the per cent growth by weight. Templeman (1940) has previously shown that the absolute increase in weight per molt of the American lobster is greater with an increase in size. An American lobster 6" weighing 3.5 oz. gains 2 oz. per molt, (5.7%), while a 14.5" lobster weighing 55 oz. gains 22 oz. per molt, (4.0%). Weight stability in *Panulirus* is reached earlier in smaller animals than in large ones. The period at which the skeleton is fully hardened and at which time growth of the tissues is virtually completed (Late Stage C of Drach, 1939) must be utilized in determining the per cent growth by weight. Earlier stages in the molting cycle, A, B, or early C, will give fluctuating results simply because there is a rather steady increase in weight up to Late Stage C (28 days) in *Panulirus*.

Growth by length

Growth in length is determined by the growth of the epidermis, which retracts from the old skeleton and increases its cell number or size or both about ten to fourteen days before shedding occurs in the summer months. It is at this time of retraction that the epidermis grows before the new soft skeleton begins to be deposited. Increase in length may be noted within an hour following ecdysis. By this time, the new soft skeleton has expanded to the point at which *Panulirus* reaches a size which it will retain until the following molt.

The per cent growth in length per molt for the various size classes is listed in Table V—a. It might be pointed out at this time that Tables V—a and V—b represent two different groups of animals.

It will be noted that there is a greater per cent growth by length per molt in smaller than in larger animals. This has also been observed in *Homarus americanus* by Templeman (1936a, 1940), Mackay (1926, 1929); in *Cancer magister* by Mackay and Weymouth (1935); in *Panulirus japonicus* by Kinoshita (1934)

TABLE V

V—a Per cent Growth by Length per Molt				V—b Gain in Carapace Length per Molt	
Carapace length (mm.)	Number of animals	Mean per cent growth by length per molt \pm Standard Error of the Mean	Calculated per cent growth per year based on number of molts per year (Tables III, VI)	Number of animals	Average (mm.) gain in carapace length per molt \pm Standard Error of the Mean
80-89	72	2.5 \pm 0.5	8-10	106	2.6 \pm 0.2
70-79	73	3.2 \pm 0.3	10-16	131	2.8 \pm 0.1
60-69	53	4.4 \pm 0.4	13-18	102	3.1 \pm 0.2
50-59	21	5.8 \pm 0.7	23-29	45	3.2 \pm 0.2
40-49	15	8.9 \pm 0.8	45	27	3.6 \pm 0.5

and Nakamura (1940). This difference observed in the laboratory does not appear to be due to significant differences in the gain of carapace length per molt from one size group to the next, but appears to be due to the fact that a smaller animal increasing its carapace length the same amount as a larger one (Table V—b) shows a greater per cent growth by length. There is a tendency, though not a significant one, for the smaller animals (40-59 mm. class) to increase their carapace length more per molt than the larger animals (Table V—b).

A few animals of the first four size groups (50-89 mm. carapace length) were successfully maintained for one year in the laboratory (Table VI). The number of molts, total number of mm. gained, and the per cent increase in length per year were determined. The results observed here serve as a rather good cross-check on information obtained in Table V—a and V—b from other animals.

Molting without growth

That growth by length does not necessarily accompany molting, was evidenced in some laboratory-maintained animals. Molting without growth or negative growth has also been observed in *Panulirus argus* maintained in live cars or wire

enclosures, under what this author considers as extremely poor conditions, by Marshall (1945) and Dawson and Idyll (1951). Within a period of almost two years and out of a total number of nearly 500 laboratory animals of various sizes, 27 were observed to undergo no increase in length following the first laboratory molt. Five of the 27 animals decreased in length by one mm. following molt. Seventeen of the 27 lobsters were obtained from a small, overcrowded lobster pound in which food was scarce and in which, as a result of overcrowding, most of the animals had autotomized some pereopods as well as antennae. Autotomy, as a result of handling, was occasionally observed in animals brought in from the field, 10 of which are included in the 27 mentioned above. That loss of appendages markedly affects the growth of the animal as a whole was demonstrated in the American lobster by Emmel (1904, 1906). He found that when regeneration occurs, the regenerating appendages are favored over increase in body length at the first molt after injury, and that regeneration tends to lengthen the intermolt period. A previous history of unfavorable environmental conditions, such as insufficient food, overcrowding and autotomy of appendages, did not result in growth at the first molt in the laboratory, although subsequent molts by these animals were accompanied by good growth.

TABLE VI

Growth in length of animals maintained for one year in the laboratory

Class	Number of animals	Number of molts per year	Carapace length gain (mm.) per year	Mean per cent increase in length \pm Standard Error of the Mean
80-89	13	3-4	9.1	10.7 \pm 1.0
70-79	15	3-5	9.7	13.2 \pm 0.9
60-69	13	3-4	12.2	19.1 \pm 1.1
50-59	2	4	11.0	21.2 \pm 2.0

SUMMARY

1. In *Panulirus argus*, premolt animals may be detected by the appearance of a resorptive or ecdysial line along the branchiostegites.
2. One of the most obvious external changes in *Panulirus* a few hours before ecdysis is the swollen condition of the intersegmental membranes.
3. Five to fifteen minutes preceding ecdysis, animals of 80-89 mm. carapace length increase their body weight by approximately 10%. This weight increase begins four to six hours preceding ecdysis and is entirely due to water absorption. There is a loss of weight following ecdysis due to loss of the exuviae. Within a few hours following molt, the weight of the individual begins to rise and continues to do so until a maximum is reached at 28-35 days. The water content begins to rise the day preceding molt, reaches its highest peak (11% above the intermolt value of 71%) one day following molt, slowly declines but does not return to its intermolt value before 28-35 days. At this period the animal has fully calcified its new skeleton, and apparently all growth of soft tissues is completed. Weight stability is not attained in 80-89 mm. carapace length animals until 28-35 days following molt.

4. Due to resorption from the ecdysial line along the branchiostegites and resorption from an articulating condyle connecting the branchial chamber to the posterior edge of the branchiostegites, progressive swelling and lateral expansion of the thorax is allowed.

5. Turgidity within the new stomach causes considerable pressure to be exerted on the surrounding regions and results in the progressive swelling and lateral expansion of the thorax preceding ecdysis. This is due to a gas which appears between the old stomach lining and the new.

6. Photographs and captions depict ecdysis in *Panulirus*.

7. The molting process appears to be directly correlated with water temperature. In Bermuda average monthly water temperatures range from 17° in February to 29° C. in August. Little molting occurs in the months of December through April, during which time the water temperatures are lowest. Water temperatures of 22° C. in May are sufficient to initiate molting. The number of molting individuals in the laboratory population increases throughout the summer months with a maximum in June, July, August, and September, at which time the highest water temperatures of 28–30° C. are reached. This means that the inter-molt periods are shortest during the summer months. The number of molting individuals during late fall declines, as temperatures decrease. Water temperatures of 19° C. or below, however, are required to stop the molting process in the winter. Decrease in molting frequency in the fall seems to be a consequence of decreased metabolism.

8. The growing period of the Bermuda lobster appears to be limited effectively to approximately seven months in the laboratory (May–November).

9. Smaller individuals grow more rapidly in the summer months than do larger individuals. Although the summer intermolt periods are shorter in smaller than in larger animals, the actual number of molts observed during a period of one year in four of the size groups maintained in the laboratory (50–89 mm. carapace length) proved to be approximately the same. An average of four molts per year was observed in these groups. As winter months approach, the smaller as well as the larger animals cease to molt and grow.

10. The smaller the animals, the greater the per cent growth by weight. Larger animals, however, gain more actual weight than smaller animals per molt.

11. There is a greater per cent growth by length per molt in smaller than in larger animals. The difference observed between larger and smaller animals is an apparent one because a smaller animal increasing its carapace length the same amount as a larger one shows a greater per cent growth by length.

12. Growth by length does not necessarily accompany molting. This was evidenced in some laboratory-maintained animals. In virtually all of these cases the environmental conditions of the individuals were poor.

LITERATURE CITED

- BAUMBERGER, J. P., AND J. M. D. OLMSTEAD, 1928. Changes in osmotic pressure and water content of crabs during the molt cycle. *Physiol. Zool.*, **1**: 531–544.
- BRADSTOCK, C. A., 1950. A study of the marine spiny crayfish *Jasus lalandii* (Milne-Edwards). *Zool. Publ. Victoria Univ. College*, **7**: 1–38.
- CHALLENGER, T., 1943. The story of the crayfish. *Tasmanian J. of Agriculture*, **14**: 51–55.
- CRAWFORD, D. R., AND W. J. J. DE SMIDT, 1922. The spiny lobster, *Panulirus argus*, of southern Florida: Its natural history and utilization. *Bull. of Bur. Fish.*, **38**: 281–310.

- DAWSON, C. E., AND C. P. IDYLL, 1951. Investigations on the Florida spiny lobster *Panulirus argus* (Latreille). *State of Florida Board of Conservation Technical Series*, 2: 6-39.
- DRACH, P., 1939. Mue et cycle d'intermue chez les crustacés décapodes. *Ann. Inst. Oceangr.*, 19: 103-391.
- DRACH, P., 1949. Périodes de mue chez un Crustacé à croissance lente (*Xantho floridus* Montagu) dans le district septentrional de son aire de reproduction. *C. R. Acad. Sci.*, 228: 128-130.
- EMMEL, V. E., 1904. The regeneration of lost parts in the lobster. Thirty-fifth annual report of the Commission of Inland Fisheries of R. I. Special Paper No. 20: 81-117.
- EMMEL, V. E., 1906. The relation of regeneration to the molting process of the lobster. Thirty-sixth Annual Report of the Commission of Inland Fisheries of R. I. Special Paper No. 27: 257-313.
- FISHER, R. A., 1948. Statistical methods for research workers. 10th ed. Hafner Pub. Co., Inc., New York.
- GUYSELMAN, J. B., 1953. An analysis of the molting process in the fiddler crab, *Uca pugnator*. *Biol. Bull.*, 104: 115-137.
- HERRICK, F. H., 1895. The American lobster. *Bull. U. S. Fish Comm.*, 15: 1-252.
- KINCAID, F. D., AND B. T. SCHEER, 1952. Hormonal control of metabolism in crustaceans. IV. Relation of tissue composition of *Hemigrapsus nudus* to intermolt cycle and sinus gland. *Physiol. Zool.*, 25: 372-380.
- KINOSHITA, T., 1934. On the artificial propagation of *Panulirus japonicus* and some account of its larvae. *Proc. 5th Pan. Pacific Sci. Cong.*, 5: 4191-4193.
- MACKAY, D. A., 1926. Rate of growth of young lobsters. *Science*, 64: 257.
- MACKAY, D. A., 1929. Larval and postlarval lobsters. *Amer. Nat.*, 63: 160-170.
- MACKAY, D. C. G., AND F. W. WEYMOUTH, 1935. The growth of the Pacific edible crab, *Cancer magister* Dana. *J. Biol. Board Canada*, 1: 191-212.
- MARSHALL, N., 1945. The molting without growth of spiny lobsters, *Panulirus argus*, kept in a live car. *Trans. Amer. Fish. Soc.*, 75: 267-269.
- NAKAMURA, S., 1940. Ecological studies on the spiny lobster *Panulirus japonicus* (V. Siebold) with special reference to its conservation. *J. Imper. Fish. Inst.*, 1: 101-113.
- PEARSON, J. C., AND W. W. ANDERSON, 1946. Spiny lobster. *U. S. Fish and Wildlife Service Fishery Leaflet*, 142: 1-4.
- SMITH, F. G. W., AND C. A. GATHMAN, 1948. The spiny lobster and scalefish industry of British Honduras. Report from the Univ. Miami Mar. Lab. 1-29.
- SUTCLIFFE, W. H., JR., 1952. Some observations of the breeding and migration of the Bermuda spiny lobster, *Panulirus argus*. *Proc. Gulf Carib. Fish Inst.*, Fourth Annual Session: 64-69.
- SUTCLIFFE, W. H., JR., 1953. Further observations on the breeding and migration of the Bermuda spiny lobster, *Panulirus argus*. *J. Mar. Research*, 12: 173-183.
- TEMPLEMAN, W., 1936a. Local differences in the life history of the lobster (*Homarus americanus*) on the coast of the maritime provinces of Canada. *J. Biol. Board Canada*, 2: 41-87.
- TEMPLEMAN, W., 1936b. The influence of temperature, salinity, light and food conditions on the survival and growth of the larvae of the lobster (*Homarus americanus*). *J. Biol. Board Canada*, 2: 485-497.
- TEMPLEMAN, W., 1940. The life history of the lobster. Newfoundland Govt. Dept. of Nat. Resources Fisheries Service Bull., No. 15: 1-42.
- TRAVIS, DOROTHY F., 1951a. Calcium metabolism in the decapod Crustacea. Thesis for Ph.D. degree, Radcliffe College.
- TRAVIS, DOROTHY F., 1951b. Early stages in calcification of the skeleton of *Panulirus argus* Latreille. *Anat. Rec.*, 111: 124.
- TRUITT, R. V., 1939. The blue crab. Contribution No. 27 from the Chesapeake Biological Laboratory: 10-37.
- VITZOU, A. N., 1882. Recherches sur la structure et la formation des teguments chez les crustacés décapodes. *Arch. Zool. Exp. et Gén., Série I*, 10: 451-576.
- YONGE, C. M., 1932. On the nature and permeability of chitin. I. The chitin lining of the foregut of decapod Crustacea and the function of the tegumental glands. *Proc. Roy. Soc. Lond., Ser. B*, 111: 298-329.